

# ON PREDATOR DETERRENCE BY PRONOUNCED SHELL ORNAMENT IN EPIFAUNAL BIVALVES

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**ABSTRACT.** Laboratory experiments, undertaken to determine the effectiveness of pronounced shell ornament in epifaunal bivalves against predatory shell boring by subtropical muricid gastropods and extraoral feeding by asteroids, suggest that natural and artificial spines deter muricid predators from attacking ornamented areas of the bivalve shell but do not have a similar effect upon predatory asteroids. These findings are discussed in relation to the extant and often highly spinose cementing bivalve families Spondylidae and Chamidae. The adaptive radiation of the Muricidae in the Albian may have resulted in selection for highly ornamented epifaunal bivalve taxa in shallow, warm water environments where the epifaunal habit renders sessile prey particularly vulnerable to attack by roving durivorous predators. The ability to produce spines, however, was already apparent in ancestral Pectinoida in the late Palaeozoic. It is concluded that the pronounced shell ornament of the free valves of warm water cemented epifaunal bivalve taxa is functional against shell boring muricids. Other hypothesized functions are discussed briefly.

FOR many years it has been argued that shell ornament in bivalved molluscs is directly related to the mode of life of the animal. Thus, shallow infaunal taxa display sculptures that are interpreted as acting as aids to burrowing or as stabilizers for life within soft substrata (Stanley 1970), and cementing epifaunal taxa produce commarginal lamellae or spines on the 'lower' valve as aids to attachment to hard substrata (Stenzel 1971). There have been various hypotheses for the function of spines and commarginal lamellae on the 'upper' free valve of cementing pleurothetic epifauna. It has been suggested, for example, that ornament serves to increase the effective strength of the shell and thus defend it against predators (Vermeij 1987). It has also been proposed that ornament acts to attract the growth of epibionts to the shell. The latter may discourage predation by visually camouflaging the shell or chemically masking secreted metabolites that may act as cues to potential predators (Vance 1978; Feifarek 1987). Ornament may also provide protection for sensory outposts of mantle tissue (by analogy with brachiopod soft part morphology) (Rudwick 1965; Stenzel 1971), or act to deter rasping by certain grazers which may over time erode and weaken the shell. Finally, both spines and commarginal lamellae may act as direct defences against predation (Kauffmann 1969; Vermeij 1987). It is this last hypothesis on which the present study is focused. Historically, however, both the nature of such defences, and the identity of the predators which they may deter, have been far from clear. As Harper and Skelton (1993*a*) have pointed out, much of the literature concerning shell ornament in bivalves has been based upon anecdotal evidence.

The great majority of shell ornament studies have concentrated on infaunal taxa and their adaptations to life within soft substrata (e.g. Stanley 1970, 1981, 1988; Wilson 1979; Watters 1993). However, some work has shown that predation by naticid gastropods may be an important selective force operating on the functional design of certain shallow infaunal bivalve groups, especially in the Indo-Pacific (Ansell and Morton 1983). The effects of shell ornament on other predatory methods, such as smothering by naticids (Ansell and Morton 1987), foraging by crabs, asteroids and birds (Carter 1968; Ansell 1969), and fish predation, have received little attention. Very little evidence has been presented concerning the possible anti-predatory effects of epifaunal bivalve shell sculpture in relation to a variety of predatory methods, including shell boring by muricid gastropod predators and extraoral feeding by asteroids, both subjects of the present study.

Muricids are known to exert heavy predation pressure on organisms in many shallow warm

temperate, subtropical and tropical rocky shores and coral reefs (Taylor 1976, 1978). In these environments, spinose epifaunal prey taxa may be an important component of the intertidal and subtidal megafauna. Jackson (1977), for example, in his studies of Jamaican reefs, stated that more than 50 per cent. of spondylid, dimyid and chamid mortalities may be caused by shell boring muricid gastropods. Recently, a possible defensive rôle for the pronounced shell ornament of the intertidal oyster *Saccostrea cucullata* (Born) has been suggested by Taylor (1990), who noted that in Hong Kong the marginal spines of this species may hinder edge-boring by muricids. Preliminary experimental observations of Harper and Skelton (1993a) on the same species also suggested that spines are directly effective at deterring muricid predatory activity; they stressed the potential importance of the rise of the shell boring muricids in the early Cretaceous as a factor influencing bivalve defensive traits. Apart from studies such as that of Harper (1994), little work has been published on bivalve predation by subtropical and tropical extraoral feeding asteroids.

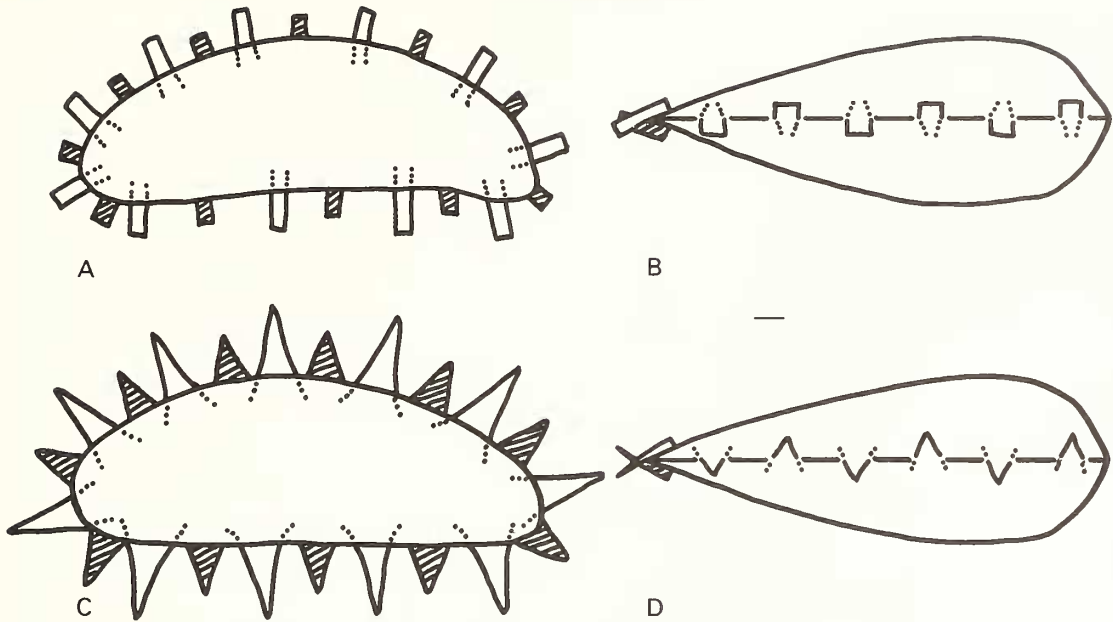
Two epifaunal cementing bivalve families, Spondylidae and Chamidae, are of particular interest in the present analysis of the direct inhibitory effect of shell ornament on predators. Although unrelated, both have a wide distribution in warm temperate, subtropical and tropical shallow waters, particularly on rocky shores and reefs (Zavareï 1973; Bernard 1976). Stanley (1970) noted that the spinose ornamentation of these groups, particularly the spondylids, may serve as a defensive adaptation. He considered reef fishes potentially important but did not demonstrate experimentally a link between epifaunal bivalve ornamentation and predation. Likewise, Logan (1974) has suggested that the spines of *Spondylus americanus* Hermann, a species living on the Bermuda Platform, perform a protective function, but did not state which predators would be deterred. This study presents evidence, through manipulative experiments, that spines on bivalve shells may directly hinder a variety of subtropical muricid gastropod predators, but do not have a similar effect against a subtropical extraoral feeding asteroid. The significance of these findings is discussed.

The terminology used to describe shell surface structures and ornamentation has seldom been rigorously applied in the literature. A 'spine' is here defined as a calcareous projection, perpendicular, oblique or subparallel to the general surface of the shell, that arises as a result of the combination of radial and concentric elements of shell growth (Cox 1969), and whose height is greater than that of the shortest dimension of its base. For structures where the basal diameter is equal to or greater than the height, the term 'node' is better applied. A 'lamella' is defined as a calcareous projection, perpendicular, oblique or subparallel to the general surface of the shell, that arises with varying degrees of radial expression but always commarginal with the commissure, and whose height is greater than that of the basal thickness. For structures where the basal thickness is equal to or greater than the height, the term 'commarginal ridge' is better applied.

#### MATERIALS AND METHODS

To determine the effectiveness of pronounced shell ornamentation in bivalves against predation by shell boring muricids and an extraoral feeding asteroid, a series of experiments was conducted on living animals in flow-through Perspex aquaria at the Swire Institute of Marine Science, Cape d'Aguilar, Hong Kong, from May to July 1995. Over this period, aquarium seawater temperatures reflected those in the field, with an average of  $25\text{ }^{\circ}\text{C} \pm 2\text{ }^{\circ}\text{C}$ . Bivalve prey were offered as a simple choice between ornamented and unornamented individuals (Experiments 1 to 3) or with varying degrees of shell ornamentation (Experiment 4). Different forms of artificial sculptural attachments were produced to form spinose shells in Experiments 1, 3 and 4, and the effects of natural ornament were observed in Experiment 2.

For prey bivalves, the mytilid *Perna viridis* (Linnaeus) was collected intertidally from a pier in the Tolo Channel (New Territories), the mytilid *Septifer virgatus* (Wiegmann) intertidally from the exposed eastern shore of Cape d'Aguilar (Hong Kong Island), and the chamid *Chama reflexa* Reeve subtidally from Hoi Ha Wan (eastern New Territories). In shallow subtidal and low intertidal

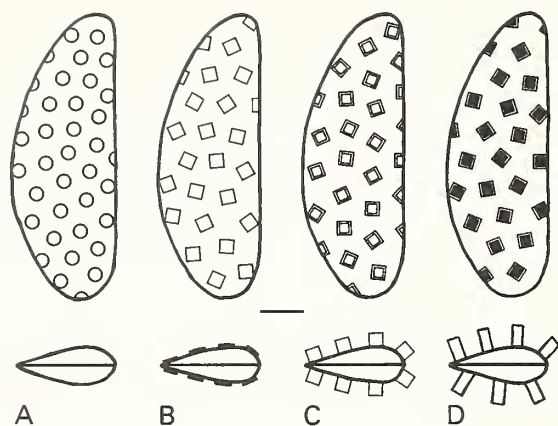


TEXT-FIG. 1. Diagrammatic representation of artificial 'spines' attached to mussel shells in Experiments 1 and 3. A-B, lateral and marginal views of polyethylene 'spines' attached to *Septifer virgatus* offered to *Thais luteostoma* as prey in Experiment 1. C-D, lateral and marginal views of 'spines' attached to *Perna viridis* cut from mussel shell, offered to *Coscinasterias acutispina* as prey in Experiment 3. Scale bar represents 1 mm (A-B) or 2 mm (C-D).

areas around many rocky shores in Hong Kong, *C. reflexa* cements to large boulders, often on their undersides or in crevices (pers. obs.). At the collection site, they were often found aggregated into dense clumps in crevices in the vertical walls of a small jetty.

The shell boring muricid predators *Thais luteostoma* Holten, *T. clavigera* Kuster and *Morula musiva* Kiener, and the extraoral feeding asteroid predator *Coscinasterias acutispina* Stimpson were all collected from sheltered sites in Lobster Bay (Cape d'Aguilar). The asteroids form an important component of the epifauna at the collection site and may feed opportunistically (Harper 1994). The muricid *Chicoreus microphyllus* Lamarck was collected from Hoi Ha Wan. *C. microphyllus*, *T. luteostoma*, *C. acutispina* and *C. reflexa* were all gathered subtidally, whilst *T. clavigera*, *M. musiva*, *P. viridis* and *S. virgatus* were found in the intertidal zone.

Apart from in Experiment 4, all bivalve prey were distributed in a random manner on the base of each tank. For the duration of the experiments the byssate *S. virgatus* and *P. viridis* were not allowed to attach themselves to the floor or walls of each tank in order to reduce the possibility of variation in strength of attachment and to ensure relative homogeneity amongst predator-prey interactions. All predator sizes were recorded. In order to reduce any bias in the observations resulting from death from other possible causes, only those bivalves whose flesh had been completely removed from the shell by the predator were recorded as 'consumed' in the following experiments. Any prey that showed any signs of physical or behavioural deterioration were immediately discarded. For each experiment, predators were initially starved for one week prior to use. All experiments were run for six weeks and aquaria were checked daily. Three replicates were undertaken for each study apart from Experiment 4, with six replicates. Statistical analyses were calculated using the chi square test.



TEXT-FIG. 2. Diagrammatic representation of artificial polyethylene 'spines' attached to the lateral surface of *Perna viridis* shells offered to *Morula musiva* as prey in Experiment 4. A, lateral and posterior views of unornamented mussels dotted with cyanoacrylate as a control. B, lateral and posterior views of 1 mm high 'spines'. C, lateral and posterior views of 2 mm high 'spines'. D, lateral and posterior views of 4 mm high 'spines'. Scale bar represents 5 mm.

### Artificial spines

Artificial spines were manufactured and attached to prey bivalve shells in Experiments 1, 3 and 4. Both the form and arrangement of such spines varied according to the experiment, as described below. Apart from in Experiment 4, the process of adhering spines or dotting unornamented prey with epoxy in the laboratory lasted about one hour per specimen at room temperature. All prey, ornamented and unornamented, underwent the same period of emersion.

In the aquarium, the muricid *Thais luteostoma* appeared to be an obligate edge-borer of the prey *Septifer virgatus*, probably the result of alternative prey not being available. The artificial spines required for Experiment 1, therefore, were fixed only along the commissure of both valves, including the area of emergence of the byssus. Since the bivalve prey in this experiment were of relatively small size, and for ease of manipulation, the artificial spines were cut from polyethylene strips to a length of 5 mm, with basal dimensions of  $2 \times 2$  mm. These were fixed to the bivalves with epoxy resin (Araldite Rapid - Ciba Geigy) at 2 mm distances along the commissure so that they both radiated outwards from the margin and interdigitated by passing through the plane of the commissure at a low angle (Text-fig. 1A-B). The artificial spines were maintained at a length of 5 mm in all cases. As a control for the use of the epoxy, unornamented prey were dotted with Araldite at the same sites as artificial spine attachment in ornamented individuals. Most spines remained secure for the duration of each relevant experiment. If any became dislodged, prey were replaced by newly prepared individuals.

Sculptural augmentation in Experiment 3 consisted of adhering artificial spines all around the commissure of the prey shell, in a similar arrangement to that of Experiment 1, except that, because the prey used in this instance were generally larger than *S. virgatus*, it was possible to cut the spines from dead *Perna viridis* shells with a craft saw, instead of from polyethylene strips. Spines produced in this way were cut to a length of approximately one-third of the length of the shell along the axis of greatest growth, and were attached with epoxy resin. Their natural curvature resulted in interdigitation across the plane of the commissure (Text-fig. 1C-D). This arrangement was chosen for two reasons: (1) the resulting spines were particularly sturdy when fixed and (2), as the mussels are orthothetic in life, a roving predator is likely to come into contact with the margins of the valves, rather than the sides, particularly on sense mussel beds. As a control, epoxy resin was also applied to the shells of unornamented prey so that any differences in asteroid feeding behaviour by, for example, the presence of adhesive chemically masking metabolic cues secreted by the mussels, would apply to both ornamented and unornamented prey alike.

In Experiment 4, artificial spines were cut at varying lengths and arranged over the whole surface of the free unattached valve of artificially cemented *P. viridis* prey. For ease of manipulation, spines were cut from polyethylene strips and attached with cyanoacrylate (Superglue-Loctite) rather than epoxy resin. This provided effective underwater strength of adhesion. The spines were spaced at

2 mm from each other on the free valve surface, mirroring the basal dimensions of the projections themselves ( $2 \times 2$  mm) (Text-fig. 2). As a control, the five unornamented bivalves were dotted with cyanoacrylate at 2 mm intervals, thus mimicking the spine distributions on ornamented individuals. All treatments covered the entire free valve from the umbo to the posterior margin. The process of attaching the spines to the shells in the laboratory lasted about ten minutes for each specimen.

The use of epoxy resin and cyanoacrylate in manipulative experiments is far from new. Harper (1991), for example, in her work on the effects of cementation on predation, has shown that daubing the shells of *Mytilus edulis* with epoxy reveals no apparent inhibitory effect on crushing predation by the crabs *Cancer pagarus* and *Carcinus maenas* or extraoral predation by the asteroid *Asterias rubens*. For the work presented here, a pilot study of drilling by *Thais clavigera* revealed no statistically significant difference in consumption between numbers of *Perna viridis* whose shell had been dotted with either epoxy or cyanoacrylate and those that had been left untouched.

### Experiment 1

This experiment was designed to show whether artificial spines had an inhibitory effect on shell boring by *Thais luteostoma*. Five *T. luteostoma* were offered 20 *Septifer virgatus* as prey. Ten of the latter were unornamented, and ten had artificial 'spines' attached to both valves all around the commissure. Any differences in the positions of bore holes in ornamented and unornamented prey were noted, and observations were made on the possible inhibitory effects of the spines themselves. All bivalves eaten were replaced with ones of similar size and state of ornamentation.

### Experiment 2

This experiment was designed to show if the natural ornamentation of the 'upper' right valve or commissural edge of the prey bivalve *Chama reflexa* inhibits boring by the muricids *Chicoreus microphyllus* and *Thais clavigera*. Two *C. microphyllus* and ten *T. clavigera* were offered 20 *C. reflexa* as prey in each tank. The numbers of each muricid species used merely reflected availability and no attempt at making any inferences about differences in the number of bore holes made by the two muricids was made. Ten bivalves were presented with their natural shell ornament intact, and ten had been filed to a smooth, unornamented finish. The natural sculpture consisted of either very small spines (up to 1.5 mm long) covering the 'upper', right valve, or a crenulate marginal lamella projecting some 2 mm from the commissure, or both. For prey which had been filed smooth, ornament was removed only from the right valve of each specimen. The left valves of all ornamented and unornamented specimens, which were covered by commarginal series of attachment lamellae except at the site of the attachment scar, were left untouched. No attempt was made to cement artificially the prey in the tanks and the bivalves were offered in random distributions and orientations. A range of prey sizes was presented and consumed individuals were replaced by ones of similar size and state of ornamentation. As in Experiment 1, the areas of boring were noted. Exact positions of bore holes are not displayed graphically, however, because of the variable shell morphology of *C. reflexa* and hence the difficulty of projecting such positions onto a standard graphic template.

### Experiment 3

This experiment was designed to show if artificial spines deter predation by the extraoral feeding asteroid *Coscinasterias acutispina*. Ten individuals of *C. acutispina* were offered 40 *Perna viridis* as prey, of which 20 were 'ornamented' and 20 'unornamented'. A random size range of prey was presented, and all bivalves consumed were replaced by individuals of similar size and ornament. Numbers of consumed individuals were recorded as well as the feeding behaviour of *C. acutispina* in order to determine any inhibitory effect that the spines may confer. Only animals with three or

more primary arms were selected for use in the study and were chosen at random for each replicate from a holding tank. As noted by Harper (1994), there is a tendency for *C. acutispina* to undergo fissiparity, and this may be a result of stress caused by aquarium confinement or by other factors, such as high levels of prey consumption. Any daughter asteroids produced in this way were immediately removed so that only ten starfishes were present in each replicate at any one time.

#### *Experiment 4*

This was essentially a prey choice study and was designed to show if increasingly spinose prey bivalves had a concomitant increasingly inhibitory effect on shell boring by the muricid *Morula musiva*. Twenty *Perna viridis* were cemented artificially to a Perspex sheet in an aquarium and presented to five *M. musiva* predators. Attachment to Perspex was effected by attaching each shell with epoxy resin by either the right or left valve. Both the choice of the valve of attachment and the orientation of each fixed mussel on each sheet were determined at random. Each replicate sheet was slotted vertically into a Perspex frame at the bottom of an aquarium tank, providing individual predator compartments with partitioning sheets of cemented prey separating each compartment. This design was considered satisfactory as it allowed the valves of the mussels to gape normally with apparently little detrimental effect upon feeding and respiration. Of the 20 *P. viridis* on each sheet partition, five were unornamented, five were ornamented with 1 mm long artificial spines, five with 2 mm long spines and five with 4 mm long spines. All artificial spines were applied to the free valve in each case and, as in Experiment 1, the spines were cut from polyethylene strips, with a basal area of 2 × 2 mm. Artificial attachment of prey to the Perspex sheets did not result in any apparent detrimental effect to normal valve gaping. Moreover, despite this treatment, all the prey in this experiment continued to produce copious byssus threads, suggesting that they were behaving normally. These threads were scraped away from their attachment to the sheet to reduce the possibility of predators being caught and immobilized by them, as has been reported for other mytilids (e.g. Petraitis 1987; Wayne 1987; Day *et al.* 1991), which may have biased the results.

In each replicate, consumed prey were replaced in the same manner as the experiments above until five or more of each particular ornament type were eaten. Subsequently, all remaining mussels of the same type were removed, leaving a reduced amount of sculptural possibilities to be tackled by *M. musiva*. This process was repeated until termination of the experiment when prey preferences could be determined. Consumed prey were also analysed for position of bore holes.

## RESULTS

#### *Experiment 1*

*Thais luteostoma* versus *Septifer virgatus* with artificial marginal spines. The null hypothesis that equal numbers of ornamented and unornamented prey should be consumed is rejected using the chi square test at a 95 per cent. confidence level (Table 1). Very few spinose bivalves were tackled and, of those that were, there was no evidence of any predator behavioural modification resulting in changes in bore hole positioning. All bore holes, for both spiny and non-spiny prey, were made at the commissural edge and the vast majority located antero-ventrally in the area of the emergence of the byssus (Text-fig. 4A). A byssal gape is present to a greater or lesser degree in all mytilids and, when not permitted to attach to a substrate, is potentially a particularly vulnerable area because it may allow direct entry to the body cavity and metabolites leached from the gape may act as chemical cues to potential predators. The method of experimentation described above is justified because it is even more likely that spines would provide effective defence if the mussels were allowed to attach normally by the byssus and become orthothetically orientated, as in life. This is especially true when shells aggregate side to side in beds and a potential predator would be presented with ornamented dorsal margins rather than the unornamented sides of the valves.

The results show that, in the aquarium, *Thais luteostoma* is an obligate edge-borer on *Septifer virgatus* and that artificial marginal spines attached to prey shells effectively inhibit predation by this

TABLE 1. Numbers of unornamented and artificially ornamented *Septifer virgatus* consumed by the muricid gastropod *Thais luteostoma* in three replicate experiments. Statistical analysis using chi square. Assuming a confidence level of 95 per cent., the null hypothesis that equal numbers of ornamented and unornamented prey are eaten is rejected for all replicates.

Replicate	A	B	C
Spiny prey consumed	2	3	3
Non-spiny prey consumed	36	34	38
Overall total	38	37	41
Predator size (mm)	36.2	36.5	32.7
<i>P</i>	≪ 0.01	≪ 0.01	≪ 0.01

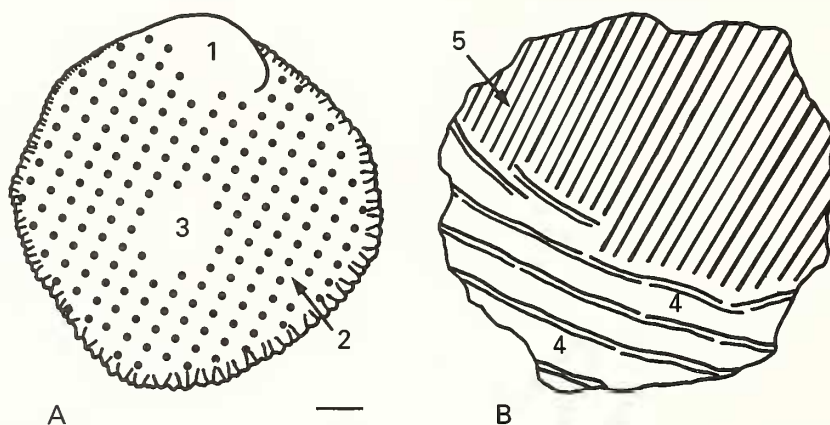
TABLE 2. Numbers of unornamented and naturally ornamented *Chama reflexa* consumed by the muricid gastropods *Chicoreus microphyllus* and *Thais clavigera* in three replicate experiments. Statistical analysis using chi square. Assuming a confidence level of 95 per cent., the null hypothesis that equal numbers of ornamented and unornamented prey are consumed cannot be rejected, and, at the same confidence level the null hypothesis that equal numbers of left and right valves are bored cannot be rejected in two of the three replicates.

Replicate	A	B	C
Ornamented prey consumed	11	16	10
Unornamented prey consumed	14	11	15
Total consumed	25	27	25
<i>P</i>	≥ 0.05	≥ 0.05	≥ 0.05
Right valves bored	10	5	11
Left valves bored	10	17	9
<i>P</i>	≥ 0.05	< 0.01	≥ 0.05

muricid. No attempt was made to bore the sides of any valves and no incomplete bore holes were recorded. It is interesting to note that most boring resulted in damage to both valves either side of the thin byssal gape in any one individual, but the periostracum often remained intact along the commissure (Text-fig. 4A). This provides additional evidence to that already published that the thick periostracum of many mytilids, including that of *S. virgatus* at a thickness of 60  $\mu\text{m}$  (Harper 1997), is difficult to penetrate by gastropod borers and may constitute a defensive adaptation (Harper and Skelton 1993b). An inspection of those spinose mussels whose defences had been overcome by *T. luteostoma* showed that one or more spines had been dislodged, suggesting that if all spines had remained completely intact, there would have been even less predation of ornamented individuals. In only one prey individual were all the spines intact after a successful predatory attack (Text-fig. 4B). Aquarium observations revealed that, after making contact with the prey, the muricids would hold the mussels with the foot and orientate them so that the byssal gape was innermost, presumably so that the radula and Accessory Boring Organ could be applied in this area. Physical manipulation of prey by muricid gastropods has not been previously described. Many ornamented and unornamented prey were held in this way, suggesting that chemical stimuli, which have been shown to be a causal factor in attracting muricid gastropods to potential victims (Kohn 1961; Pratt 1974; Carriker 1981; Cross 1983; Williams *et al.* 1983), had not been impaired by the experimental technique, and the rejection of spinose prey was a result of behavioural responses provoked by unfavourable subsequent tactile stimulus. Large numbers of unornamented prey were consumed, despite being dotted with epoxy, and therefore it is concluded that the presence of spines alone is responsible for inhibiting predatory activity.

TABLE 3. Number of bore holes made in different areas of the shell of *Chama reflexa* by the muricid gastropods *Chicoreus microphyllus* and *Thais clavigera* in three replicate experiments.

	Replicate A		B		C	
	Valve Left	Right	Left	Right	Left	Right
Umbonal	—	0	—	0	—	1
Median (ornamented)	—	0	—	0	—	0
Median (unornamented)	1	10	1	5	0	10
Inter-lamellar	2	—	4	—	4	—
Area of attachment	7	—	12	—	5	—
Total	10	10	17	5	9	11



TEXT-FIG. 3. Generalized representation of the bivalve *Chama reflexa* offered to *Chicoreus microphyllus* and *Thais clavigera* in Experiment 2. A, right valve with crenulate marginal lamella, divided into three areas: (1), umbonal; (2), median (ornamented); (3), median (unornamented). Dotted area indicates spinose valve surface. B, left valve, divided into two areas: (4), inter-lamellar; (5), area of attachment. Hatched area indicates flat attachment scar. Scale bar represents 2 mm.

### Experiment 2

*Chicoreus microphyllus* and *Thais clavigera* versus *Chama reflexa*. The results are summarized in Tables 2 and 3. There was no significant difference between the numbers of ornamented and unornamented prey bored, and the null hypothesis that equal numbers of each should be consumed cannot be rejected with chi square analysis at a 95 per cent. confidence level. Upon closer examination, however, some important observations may be made. Table 3 shows the number of times specified areas of the shell were bored successfully for both left and right valves. Five areas are described (Text-fig. 3). For the right, or 'upper' valve, these are: umbonal, median (ornamented) and median (unornamented) (Text-fig. 4c). For the left, or 'lower' valve these are: inter-lamellar and area of attachment. Of the ornamented *C. reflexa* prey, the sculpture on certain areas of the surface of the right valve may be less expressed in some individuals than in others. Bore holes made at these sites are described as median (unornamented). The natural ornament may also have been eroded from the umbonal region during ontogeny, resulting in possible reduced defence in this area (Text-fig. 3A). For the left valve, boring was not observed to have occurred through the



attachment lamellae of the left valve, but only in the commarginal inter-lamellar spaces between adjacent elements (Text-fig. 3B). Table 3 reveals that on no occasion was a bore hole successfully made in a truly ornamented area of a prey shell. The majority of bore holes were either made in the area of attachment of the left valve or unornamented areas of the right valve. In the chamids' natural habitat, boring of the left valve is extremely unlikely to occur unless the bivalve has become forcibly detached, and it is not surprising that the muricids should attack unornamented areas of left valves in the aquarium, in particular the potentially weak area of attachment. However, although the majority of left valves were thinnest in this area, the fact that other areas of both left and right valves were bored, including inter-lamellar areas and the relatively thick right valves, suggests that the degree of ornament expression is the primary determinant of the choice of bore hole site rather than valve thickness. It seems reasonable to suggest that pronounced marginal ornament exhibited by potential prey will additionally afford a degree of protection from boring near the valve edges, in much the same way as the artificial marginal spines of *S. virgatus* in Experiment 1. It may be concluded that the shell spines of lamellae of *C. reflexa* offer a degree of defence against boring by muricids.

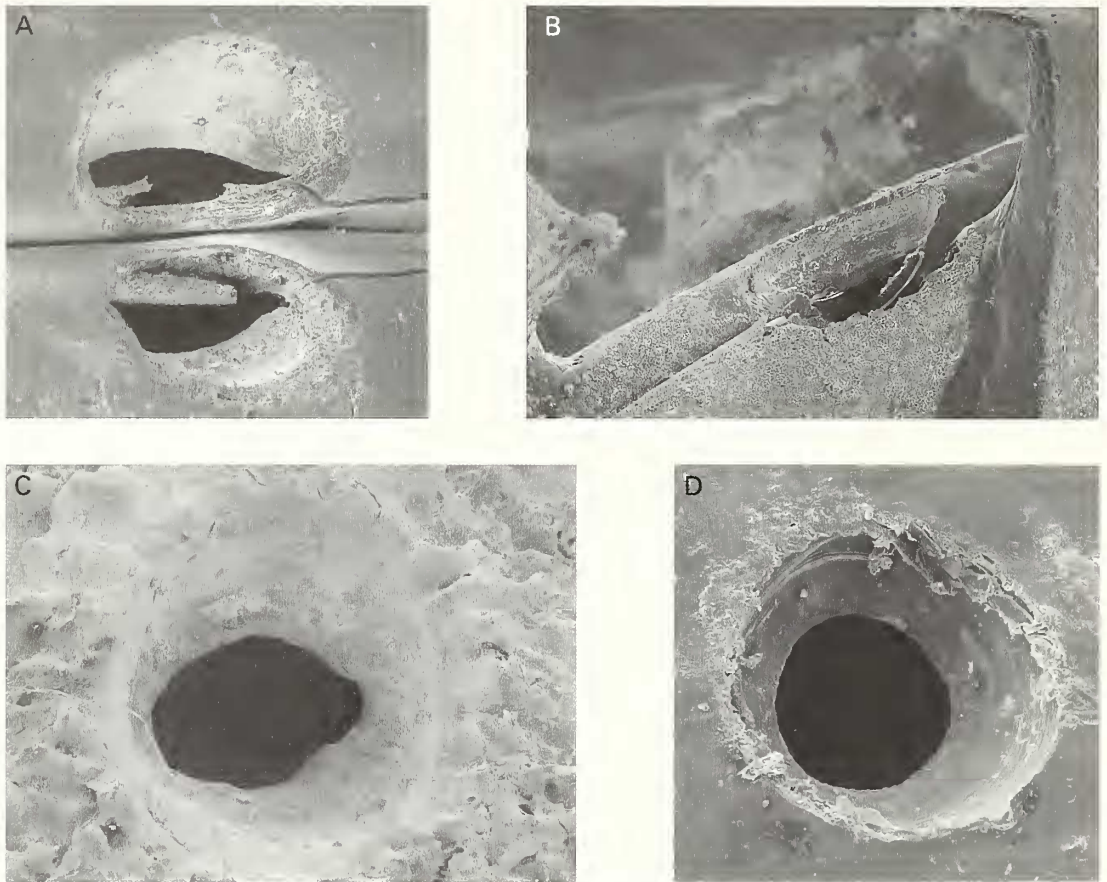
TABLE 4. Numbers of unornamented and artificially spinose *Perna viridis* consumed by the extraoral feeding asteroid *Coscinasterias acutispina* in three replicate experiments. Statistical analysis using chi square. Assuming a confidence level of 95 per cent., the null hypothesis that equal numbers of ornamented and unornamented prey are consumed cannot be rejected.

Replicate	A	B	C
Ornamented prey consumed	25	17	46
Unornamented prey consumed	28	24	41
Overall total	53	41	87
<i>P</i>	≥ 0.05	≥ 0.05	≥ 0.05

### Experiment 3

*Coscinasterias acutispina* versus *Perna viridis*. The results are summarized in Table 4. They reveal that there was no significant difference in the numbers of spinose and non-spinose mussel prey consumed. The null hypothesis that equal numbers of each should be eaten could not be rejected using chi square analysis at a 95 per cent. confidence level. The larger number of bivalves eaten in replicate C can probably be attributed to the larger mean size of the starfishes available for this replicate.

In the aquarium, the feeding behaviour of *C. acutispina* is typical of other extraoral feeding asteroids. It assumes a hunched posture over the prey bivalve so that the stomach lobes can be extruded into the shell after prising the valves apart. For mussel prey, the stomach lobes may be extruded into the body cavity through the narrow byssal gape. This has been reported for other genera (Feder 1955; Lavoie 1956; Carter 1968). In contrast to the experiments with muricid borers presented above, *C. acutispina* showed no statistically significant preference for the non-spinose mussels offered. In general, the predatory behaviour of the starfish did not differ when it was confronted by ornamented or unornamented prey. Such behaviour was characterized by an initial encounter with the prey and subsequent manipulation so that the ventral margins, and in particular the byssal gape, were orientated towards the oral region of the predator. In this experiment, the spines of some of the artificially ornamented mussels had been removed by the predators. It is, therefore, probable that the ornament was removed during the process of manipulation or possibly prising of the valves, although the latter was not directly observed. Attached marginal spines were up to one-third the length of the axis of greatest growth in any one individual and, because they



TEXT-FIG. 4. Scanning electron micrographs of muricid bore holes in prey bivalve shells. A, hole bored by *Thais luteostoma* through posterior extremity of the byssal gape of *Septifer virgatus*;  $\times 43$ . B, single occurrence of a bore hole made by *Thais luteostoma* between intact artificial 'spines' (seen left and right in picture) attached to *Septifer virgatus*;  $\times 33$ . C, bore hole made by *Chicoreus microphyllus* in median area of a left valve of *Chama reflexa* lacking macro-ornament;  $\times 20$ . D, bore hole made by *Morula musiva* in an unornamented area between artificial 'spines' attached to the lateral surface of a *Perna viridis* shell;  $\times 45$ . Material in author's possession.

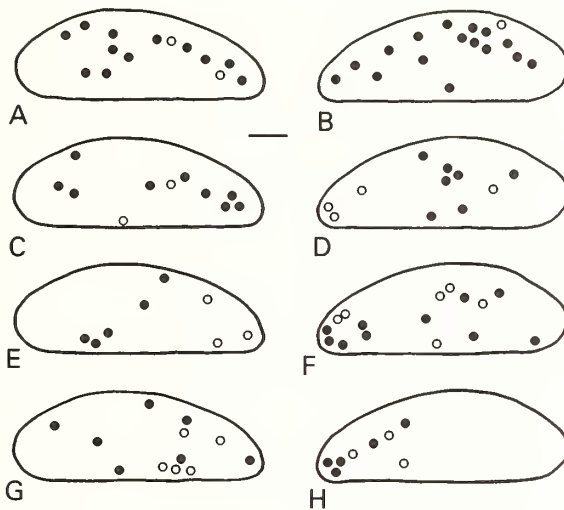
interdigitated across the plane of the commissure in those mussels whose spines remained intact throughout the feeding process, and would therefore still provide an effective barrier, it is likely that prising the valves apart a short distance would be ineffective in itself. Thus, the stomach lobes may have been extruded to at least the same length as the spines themselves in order to reach the body cavity. The above evidence reveals that *C. acutispina* is adept at dealing with different types of prey and has no difficulty in overcoming the artificially defended bivalves in this experiment.

#### Experiment 4

*Morula musiva* versus *Perna viridis*. The results of this choice experiment are summarized in Table 5. The muricid predators chose unornamented mussels as a first choice in three out of the six replicates and as a second choice in two replicates. Highly ornamented prey with 4 mm long spines were chosen only in third place in two replicates. Complete consumption of the other sculptural types, 1 mm and 2 mm spines, was more variable. The results, therefore, suggest that prey with less expressed ornament are preferred to those that are highly spinose (Text-fig. 4D).

TABLE 5. Results of Experiment 4, in which the muricid *Morula musiva* was offered a choice of *Perna viridis* prey: unornamented (NS), with 1 mm long artificial spines, with 2 mm artificial spines or with 4 mm long artificial spines in six replicate experiments. Unornamented prey were chosen as a first choice in three out of six replicates, and as a second choice in two replicates.

Replicate	A	B	C	D	E	F
First choice	1 mm	2 mm	NS	2 mm	NS	NS
Second choice	NS	—	—	NS	1 mm	—
Third choice	4 mm	—	—	4 mm	2 mm	—
Fourth choice	—	—	—	1 mm	—	—
Total prey consumed	21	11	12	20	22	10



TEXT FIG. 5. Positions of all bore holes made by *Morula musiva* in right (A, C, E, G) and left (B, D, F, H) valves of the mussel *Perna viridis*. Filled circles: holes made in non-attached 'free' valves. Hollow circles: holes made in artificially attached valves. Umbones are towards the centre of the page. A-B, holes made in valves without artificial ornament but dotted with cyanoacrylate as a control. C-D, holes made in valves with 1 mm long artificial 'spines' attached. E-F, holes made in valves with 2 mm long artificial 'spines' attached. G-H, holes made in valves with 4 mm long artificial 'spines' attached. Scale bar represents 5 mm.

Since it was necessary to allow the mussels to function as near normally as possible in this experiment, all prey were cemented for only a portion of the relevant valve so that the valve margins were raised clear of the artificial substrate. This permitted some boring in the attached valve, especially in the area of the umbo. Table 6 reveals that the percentage of bore holes made in attached valves increases from 9.7 per cent in non-spinose mussels to 40.0 per cent. in prey with 4 mm spines. This is additional evidence of the deterrent value of increasing shell ornament. The positions of all bore holes, for both attached and free valves, are shown in Text-figure 5. It is inferred from this experiment, therefore, that the primary effect of pronounced spines on the shells of epifaunal bivalves is that of hindering direct access to the general shell surface.

TABLE 6. Bore hole analysis of the four types of artificially ornamented *Perna viridis* drilled by the muricid *Morula musiva*.

Ornament type	Non-spiny	1 mm spines	2 mm spines	4 mm spines
Percentage bore holes in attached valve	9.7	27.3	37.5	40.0

## DISCUSSION

The biotic changes associated with the so-called Mesozoic Marine Revolution (M.M.R.) have been identified by Vermeij (1977, 1978, 1987) as a probable causal factor in the subsequent evolution of strengthening armour in gastropods and bivalves. The M.M.R. was characterized by an increase in the importance of a host of predatory methods and resulted not only in an increase in the development of prey armour in potentially vulnerable molluscan epifaunal taxa but also an expansion of groups escaping predators in other ways, such as those colonizing the infaunal realm (Stanley 1968; Vermeij 1978, 1987). Predatory methods, and the potential consequences of the M.M.R. for molluscan prey, have been assessed by Vermeij (1977, 1987) and Harper and Skelton (1993a). Epifaunal bivalves are particularly vulnerable to three predatory strategies: (1) 'insertion and extraction', by extraoral feeding asteroids, prising gastropods, some birds and fish, octopods, arthropods and crustaceans; (2) 'crushing', by many crustaceans, fish, arthropods and some molluscs; and (3) 'boring', by muricid and naticid gastropods and some cephalopods. It has been proposed that these three strategies became dramatically more important as a result of the M.M.R. (Vermeij 1977, 1987).

The experiments presented here were undertaken to examine the effects of two such predatory strategies: shell boring by muricid gastropods and extraoral feeding by asteroids. Both predatory groups have often been held responsible for severe predation impact on epifaunal molluscs, particularly bivalves, in subtropical-tropical and temperate shallow water environments respectively (Galtsoff and Loosanoff 1939; Hancock 1955, 1958; Taylor 1976, 1978), and thus they are particularly suitable for a study of the anti-predatory effects of epifaunal bivalve shell ornament. Cemented bivalves in particular may present themselves as potential sitting targets to muricid gastropods (Harper and Skelton 1993a).

Of the principal epifaunal cemented taxa, warm-water oysters, spondylids and chamids display a high degree of morphological plasticity, associated with the habit of cementation, and an ability to construct shells with pronounced spines and/or commarginal lamellae. The results presented here suggest that such ornament in prey taxa is itself directly effective in deterring boring by muricid gastropods. For both chamid and mytilid prey, unornamented areas of the shell are preferentially bored over ornamented areas in each of the three experiments conducted with muricid predators. Where behavioural adaptation seems to have resulted in a high degree of bore hole site specialization, for example in relation to edge-boring by *Thais luteostoma* in Experiment 1, any subsequent site modification that might have been expected when confronted by artificially ornamented prey is lacking. Thus, *T. luteostoma* does not attack the unornamented valve surfaces of *Septifer virgatus* prey and, rather than choosing new bore hole sites in mussels with marginal ornament, this predator takes advantage of the preferential site in unornamented prey (in this case the byssal gape). As new shell ornament of potential prey is formed at the commissure, it is less likely to have been eroded than sculpture formed earlier in ontogeny which cannot be repaired, and predators which attack the valve margins are likely to be at a competitive disadvantage in comparison with those that choose the bore hole site more liberally. This may help to explain why edge-boring of bivalves by muricid gastropods in the field has only rarely been reported (e.g. Morton 1994).

In contrast to the muricid predators, the subtropical extraoral feeding asteroid *Coscinasterias acutispina* is not measurably deterred by artificial spines fixed to mussel prey, even when such spines are positioned around the entire commissure, including the byssal gape. It is through a commissural gape that the stomach lobes of the asteroid are extruded. The gape may be formed mechanically by prising the valves of the prey apart a small distance or it may be a natural element of shell growth. Prising was not directly observed in the current experiment and, as prey were orientated with the byssal gape nearest the oral region of the predator, it was concluded that the stomach lobes were being extruded through this region. In a pilot study, a group of predators were removed from prey during feeding with their everted stomach lobes clearly visible. Despite the presence of large artificial marginal spines on *Perna viridis*, *C. acutispina* is clearly adept at dealing with such 'difficult' prey. It is conceivable that, if spines had been arranged over the general surface of the valves, including the commissure, manipulation of prey by the asteroid might have been more problematical. However, artificial ornament strong enough to withstand such handling could not be attached successfully on the valve surface. Moreover, as stated previously, it is the commissure of the prey bivalve that is most often heavily defended, as this is where new shell material is laid down, and thus it is the ability to extrude stomach lobes through a heavily defended commissure that is of greatest interest. Although naturally cemented bivalves do not present extra-oral feeding asteroids with natural gapes through which stomach lobes can be extruded, it is likely that prising the valves apart a small distance will create a temporary gape, and thus a potentially vulnerable area. In Experiment 3, valve prising was not directly observed but may not have been required for extra-oral feeding because of the presence of the byssal gape in the *Perna viridis* prey offered. The methodology of the present study is therefore considered satisfactory.

It has been stated by some authors, such as Vermeij (1987), that extraoral feeding asteroids are not in general a common component of the benthic megafauna on tropical and subtropical rocky shores. In contrast, muricid gastropods are often abundant and likely to exert strong predatory pressure (Taylor 1976, 1977, 1978). In these areas, therefore, the threat from muricids is potentially far more important than that of extraoral feeding asteroids. The impact of the extraoral method of attack, however, may be particularly severe in cooler waters, where asteroids often aggregate in large numbers and may devastate local epifaunal bivalve populations (Galtsoff and Loosanoff 1939; Hancock 1955, 1958). However, in cooler waters highly ornamented bivalve taxa are rare or non-existent (Nicol 1964, 1965; Harper and Skelton 1993a). It seems highly doubtful, therefore, that the presence of marginal ornament in epifaunal bivalves is functional against the extraoral method of attack, and this proposal is strengthened by the results of the experiment presented here.

To determine whether pronounced shell ornament in cementing epifaunal bivalve families, such as the unrelated Spondylidae and Chamidae, arose as an adaptation to the threat posed by muricid gastropod borers, it is necessary to demonstrate agreement between the timing of the onset of the adaptive radiation of muricids in the Albian (Taylor *et al.* 1980, 1983) on the one hand and the appearance of highly ornamented potential prey taxa on the other.

Harper and Skelton have documented the numbers of spinose and non-spinose species of the family Spondylidae from the Jurassic to the present day, and show a general increase in the percentage of spinose species over time (Harper and Skelton 1993a, fig. 3). My own unpublished data concur with their results. Despite this increase, however, it is apparent that the rise of spinose ornamentation in *Bivalvia* predates the adaptive radiation of the muricid gastropods. The ability to construct ornament was already evident in some late Palaeozoic Pectinoida, such as members of the family Pseudomonotidae. It has been proposed that the Spondylidae most probably arose from this family (Newell and Boyd 1970). In their work on Permian ostreiform *Bivalvia*, Newell and Boyd suggested that the morphological series: *Pseudomonotis* (*Pseudomonotis*)–*Pseudomonotis* (*Trematiconcha*)–*Prospendylus*–*Paleowaagia*–*Newaagia*–*Spondylus*– may represent a phyletic series. Within this series, a number of Permian species display spines and/or scales, most notably *Pseudomonotis* (*Trematiconcha*) *wandageensis* Newell and Boyd, *P. likharevi* Newell and Boyd, *Prospendylus acinetus* Newell and Boyd and *Paleowaagia cooperi* Newell and Boyd (Newell and Boyd 1970, figs 14A, 16A, 23A–G, 24A–E, 28A, 29B, G). Waller (1978) has suggested that spondylids may have evolved

from the superfamily Pectinoidea, rather than from the Pseudomonotidae. Despite the inherent difficulties associated with the assessment of phylogenetic affinities of many pteriomorph groups, ornament construction was nevertheless underway in the pectinoidan families Pseudomonotidae and Aviculopectiniae (for example, *Girtypecten* and *Clavicosta*; see Newell 1969), by the Late Palaeozoic. It is, therefore, unlikely that spinose ornamentation in pteriomorph bivalves arose initially as an adaptation to the muricid borers. It is also difficult to relate ornament to direct deterrence of other predatory methods, such as shell breakage by crustaceans. It is intuitively obvious that, to be effective against the latter group, shell spines and scales would need to be particularly well-developed, stout and strong, especially around the most vulnerable area, the commissure. Evidently, sculptural development in Permian Pectinoidea, although present in some genera, was only weakly expressed. Shell ornament in late Mesozoic and particularly Tertiary spondylids is very different (Zavarei 1973; pers. obs.). It seems reasonable to suggest that the faunal changes resulting in a rise in predation pressure concomitant with the M.M.R. was responsible for the adaptive development of large, strong spines that characterize many Mesozoic and Tertiary taxa. Such ornament may be effective against a variety of predators, but it is proposed here that muricid borers are potentially one of the most damaging, and potentially the most deterred by pronounced shell ornament, of all predatory groups.

The family Chamidae, unrelated to the Spondylidae but again adopting the cemented habit, probably evolved as a branch of the byssate family Carditidae in the Late Cretaceous (Kennedy *et al.* 1970) and the pronounced shell ornament displayed by the former group may, conceivably, have arisen as a primary adaptation against shell boring predators, especially in view of the evolution of the cemented habit from a byssate precursor. Ornament in extant ribbed carditids, where present, tends to consist of nodes or pronounced scales, but further studies need to be undertaken on the ornament of Palaeozoic and Mesozoic carditids before the geological history of ornament in the Carditidae and Chamidae can be adequately assessed. The evidence, however, seems to suggest that ornamentation of the 'upper' free valve of epifaunal groups evolved initially as a response to some factor other than direct predatory pressure, and may have become coincidentally advantageous under the harsh predatory regimes characterizing the M.M.R. (Vermeij 1977, 1987), particularly with respect to shell boring by muricid gastropods. The original primary function may or may not have been lost and, if the latter is the case, then shell spines and lamellae in extant epifaunal bivalve taxa could be considered multifunctional.

There are several possible hypotheses that may be put forward regarding the primary function of pronounced 'upper' valve shell ornament other than direct predatory inhibition which is the subject of the current study. Firstly, ornament may act to prevent the bivalve from becoming dislodged from cryptic microhabitats such as crevices. This does not apply to cementing taxa such as oysters, spondylids and chamids, although cementation to the sides of crevices may occur. However, some byssate taxa of the families Tridacnidae and Carditidae carry spine-like processes on both valves that may help to prevent dislodgement. The second hypothesis is that ornament may help to alleviate erosion. This applies potentially to both attached and unattached taxa. It has, however, never been satisfactorily demonstrated that the presence of ornament serves to increase shell strength in any way. Moreover, the spines of many widely distributed ornamented genera such as the semi-infaunal *Pinna* and *Atrina*, and certain members of the Spondylidae, such as *Spondylus linguafelis* Sowerby, are often elaborate and delicate and it is difficult to accept such an hypothesis. Erosion and endolithic boring of the shell by organisms such as clionid sponges can remove ornament from all or part of the shell surface and thus render the bivalve vulnerable to predation by muricids or crustaceans if the strength of the valve has been severely weakened, but if the ornament remains intact, it is likely the bivalve will be far more resistant to gastropod borers. Where chamids and spondylids are cemented to rocks in exposed areas, erosion of the shell may be extensive. Bernard (1976) stated that chamids living in such environments are large, thick-shelled with little ornamentation and very shallow in vertical distribution. In these areas, however, the intensity of predation is likely to be considerably less than at sheltered sites, especially for roving predators, such as muricids, that may be dislodged by wave action. In sheltered habitats, the

predation pressure is likely to be more intense and in these areas the ornament of chamids is often highly pronounced (Bernard 1976). The third hypothesis is that ornament may offer protection against the rasping activities of certain roving grazers, for example regular echinoids, feeding on algae growing on shells that may, over time, erode the shell and weaken it. The potential importance of grazing with respect to shell ornament is at present unclear. The fourth hypothesis considers spines and commarginal lamellae acting as stabilizing structures that prevent epifauna lying on soft substrates from being smothered. The spines of the extant chamid genus *Arcinella* may act in this way. This bivalve gains secondary freedom from an initial cemented phase early in ontogeny and rests on sandy or shelly substrates (Nicol 1952). The fifth hypothesis suggests that ornament may act to attract growth of epibionts on the shell, presumably by increasing the surface area of available substrate (Vance 1978; Feifarek 1987). Personal observations of the spondylid *Spondylus americanus* Hermann transferred to aquaria show that the colonizers are often algae, sponges, solitary corals, tube worms and hydroids. Epibiont growth may have a number of potentially beneficial effects. For example, biomineralizing colonizers may increase the effective strength of the shell and help to reduce erosion. Alternatively, epibionts may directly disguise the shell from visually hunting predators or may mask chemical cues released into the ambient environment by the bivalve which may serve as attractants for chemosensitive predators. There is good evidence that predatory gastropods are attracted by such cues (Carriker 1981). Some extant representatives of the families Spondylidae and Chamidae, for example *Spondylus linguafelis* and *Chama lazarus* Linnaeus, possess spines whose distal ends are highly intricate or enlarged into spatulate lamellae. It is conceivable that the consequent large surface area of such processes is particularly attractive to epibiont settlement. Such growth may provide serendipitous defence for sessile organisms such as cementing bivalves. The sixth hypothesis concerns shell ornament as structural supports for areas of sensory mantle tissue (Rudwick 1965; Kauffman 1969; Stenzel 1971). A mechanosensory or chemosensory capability may have several advantages. For example, it may provide the bivalve with an early warning system when under potential threat from an approaching predator, or it may warn against inclement environmental conditions, such as changes in turbidity or salinity. The intricate nature of the ornament of some members of the Spondylidae and Chamidae, referred to above, may indicate a corresponding intricacy of underlying mantle epithelium performing sensory functions. However, a sensory capability has only been suggested by analogy with the soft parts of brachiopods (Rudwick 1965), and comparative morphological evidence to substantiate this hypothesis in the Bivalvia has been lacking. Research is currently being undertaken by the author with regard to the hypothesized functions of pronounced shell ornament detailed above.

The formation of shell ornament in epifaunal bivalves can only proceed within the intrinsic constraints of the bivalve *Bauplan* and extrinsic constraints such as water temperature, food availability, etc. Many epifaunal taxa have demonstrated a remarkable ability to radiate morphologically, particularly in warm waters. Nicol (1965, 1967) has stated that there are very few ornamented bivalves inhabiting cool waters of high latitudes and the deep sea. What ornament is evident, is always subdued. In addition, bivalves that adopt the cemented habit are absent from the Arctic and Antarctic (Nicol 1964). In warm temperate, subtropical and tropical waters many cemented taxa, such as members of the Spondylidae, Chamidae and Ostreidae, are particularly adept at ornament construction. It is suggested here that the sculptural radiation of highly ornamented epifaunal taxa may be a result of pressures imposed by the shell boring muricids from the Albian onwards, resulting in adaptive radiations in potentially vulnerable prey lineages. Whilst the nature and intensity of predation is evidently very different in cool water, the pre-adaptations that may have otherwise permitted the formation of sculpture, such as an ability to produce extensive growth in periodic rapid phases, may also be absent. Feifarek (1987) found that the rate of growth of spines in the spondylid *Spondylus americanus* is extremely rapid, about 1 mm per day. In addition, Paul (1981) has suggested the shell of the highly spinose warm water neogastropod *Murex (Murex) pecten* Lightfoot grows by rapid episodic incrementation. It is likely that such modes of growth can only be achieved in warm water because of high growth rates which may be associated with a combination of warm water temperatures as well as an adequate food supply,

although the possibility that the effects of cold water enhance the dissolution of biogenic calcareous structures, retarding or preventing growth of pronounced ornament, must also be considered.

#### SUMMARY

Pronounced shell ornament in epifaunal bivalves has been shown to be effective at deterring shell boring muricid gastropods in aquarium experiments. No apparent inhibitory effect was observed for extraoral predation by asteroids. Gastropod deterrence may have become increasingly important with the adaptive radiation of the muricids in the Albian. Anti-boring defence may not be the sole function of pronounced shell ornament and it is likely that it arose initially for other reasons, in the family Spondylidae at least. Other hypothesized functions include, for example, attracting epibiont growth or outposts for sensory mantle tissue. These may have continued to play an important rôle for the epifaunal bivalve to the present day, despite the value that ornament has been shown to confer in deterring muricids.

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#### REFERENCES

- ANSELL, A. D. 1969. Defensive adaptations to predation in the Mollusca. 487–512. In *Proceedings of the Symposium on Mollusca, Cochin*, 2. Marine Biological Association of India, Mandapam, India.
- and MORTON, B. 1983. Aspects of naticid predation in Hong Kong with special reference to the defensive adaptations of *Bassina (Callanaitis) calophylla* (Bivalvia). 635–660. In MORTON, B. and DUDGEON, D. (eds). *Proceedings of the 2nd international workshop on the malacofauna of Hong Kong and Southern China, Hong Kong 1983*. Hong Kong University Press, Hong Kong, 681 pp.
- — 1987. Alternative predation tactics of a tropical naticid gastropod. *Journal of Experimental Marine Biology and Ecology*, **111**, 109–119.
- BERNARD, F. R. 1976. Living Chamidae of the Eastern Pacific (Bivalvia: Heterodonta). *Contributions in Science, Natural History Museum of Los Angeles County*, **278**, 1–43.
- CARRIKER, M. R. 1981. Shell penetration and feeding by naticacean and muricacean gastropods: a synthesis. *Malacologia*, **20**, 403–422.
- CARTER, R. M. 1968. On the biology and palaeontology of some predators of bivalved Mollusca. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **4**, 29–65.
- COX, L. R. 1969. General features of Bivalvia. N2–N129. In MOORE, R. C. (ed.). *Treatise on invertebrate paleontology. Part N. Mollusca 6 (I)*. Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas. 1224 pp.
- CROLL, R. P. 1983. Gastropod chemoreception. *Biological Reviews*, **58**, 293–319.
- DAY, R. W., BARKAI, A. and WICKENS, P. A. 1991. Trapping of three drilling whelks by two species of mussel. *Journal of Experimental Marine Biology and Ecology*, **149**, 109–122.
- FEDER, H. M. 1955. On the methods used by the starfish *Pisaster ochraceus* in opening three types of bivalve molluscs. *Ecology*, **36**, 764–767.
- FEIFAREK, B. P. 1987. Spines and epibionts as antipredator defenses in the thorny oyster *Spondylus americanus* Hermann. *Journal of Experimental Marine Biology and Ecology*, **105**, 39–56.
- GALTSOFF, P. S. and LOOSANOFF, V. 1939. Natural history of *Asterias forbesi*. *Bulletin of the U.S. Bureau of Fisheries*, **49**, 79–132.
- HANCOCK, D. A. 1955. The feeding behaviour of starfish on Essex oyster beds. *Journal of the Marine Biological Association of the U.K.*, **34**, 313–331.
- 1958. Notes on starfish on an Essex oyster bed. *Journal of the Marine Biological Association of the U.K.*, **37**, 565–589.
- HARPER, E. M. 1991. The role of predation in the evolution of cementation in bivalves. *Palaeontology*, **34**, 455–460.



- 1994. Molluscivory by the asteroid *Coscinasterias acutispina* (Stimpson). 339–355. In MORTON, B. (ed.). *The malacofauna of Hong Kong and Southern China III. Proceedings of the 3rd international workshop on the malacofauna of Hong Kong and Southern China, Hong Kong 13 April–1 May 1992*. Hong Kong University Press, Hong Kong, 504 pp.
- 1997. The molluscan periostracum: an important constraint in bivalve evolution. *Palaontology*, **40**, 71–97.
- and SKELTON, P. W. 1993a. The Mesozoic Marine Revolution and epifaunal bivalves. *Scripta Geologica, Special Issue*, **2**, 127–153.
- 1993b. A defensive value of the thickened periostracum in the Mytiloidea. *The Veliger*, **36**, 36–42.
- JACKSON, J. B. C. 1977. Competition on marine hard substrata: the adaptive significance of solitary and colonial strategies. *American Naturalist*, **111**, 743–767.
- KAUFFMANN, E. G. 1969. Form, function and evolution. N129–N205. In MOORE, R. C. (ed.). *Treatise on invertebrate paleontology. Part N. Mollusca 6 (I)*. Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas, 1224 pp.
- KENNEDY, W. J., MORRIS, N. J. and TAYLOR, J. D. 1970. The shell structure, mineralogy and relationships of the Chamacea (Bivalvia). *Palaontology*, **13**, 379–413.
- KOHN, A. J. 1961. Chemoreception in gastropod molluscs. *American Zoologist*, **1**, 291–308.
- LAVOIE, M. E. 1956. How seasters open bivalves. *Biological Bulletin*, **111**, 114–122.
- LOGAN, A. 1974. Morphology and life habits of the Recent cementing bivalve *Spondylus americanus* Hermann from the Bermuda Platform. *Bulletin of Marine Science*, **24**, 568–594.
- MORTON, B. 1994. Prey preference and method of attack by *Rapana bezoar* (Gastropoda: Muricidae) from Hong Kong. 339–355. In MORTON, B. (ed.). *The malacofauna of Hong Kong and Southern China III. Proceedings of the 3rd international workshop on the malacofauna of Hong Kong and Southern China, Hong Kong 13 April–1 May 1992*. Hong Kong University Press, Hong Kong, 504 pp.
- NEWELL, N. D. 1969. N335–N338. In MOORE, R. C. (ed.). *Treatise on invertebrate paleontology. Part N. Mollusca (I)*. Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas, 1224 pp.
- and BOYD, D. W. 1970. Oyster-like Permian bivalvia. *Bulletin of the American Museum of Natural History*, **143**, 219–281.
- NICOL, D. 1952. A revision of the pelecypod genus *Echinochama*. *Journal of Paleontology*, **26**, 803–817.
- 1964. Lack of shell attached pelecypods in Arctic and Antarctic waters. *The Nautilus*, **77**, 92–93.
- 1965. Ecologic implications of living pelecypods with calcareous spines. *The Nautilus*, **78**, 109–116.
- 1967. Some characteristics of cold-water marine pelecypods. *Journal of Paleontology*, **41**, 1330–1340.
- PAUL, C. R. C. 1981. The function of the spines in *Murex (Murex) pecten* Lightfoot and related species (Prosobranchia: Muricidae). *Journal of Conchology*, **30**, 285–294.
- PETRAITIS, P. S. 1987. Immobilization of the predatory gastropod, *Nucella lapillus*, by its prey, *Mytilus edulis*. *Biological Bulletin*, **172**, 307–314.
- PRATT, D. M. 1974. Attraction to prey and stimulus to attack in the predatory gastropod *Urosalpinx cinerea*. *Marine Biology*, **27**, 37–45.
- RUDWICK, M. J. S. 1965. Sensory spines in the Jurassic brachiopod *Acanthothiris*. *Palaontology*, **8**, 604–617.
- STANLEY, S. M. 1968. Post-Paleozoic adaptive radiation of infaunal bivalve molluscs a consequence of mantle fusion and siphon formation. *Journal of Paleontology*, **42**, 214–229.
- 1970. Relation of shell form to life habits of the Bivalvia (Mollusca). *Memoir of the Geological Society of America*, **125**, 1–296.
- 1981. Infaunal survival: alternative functions of shell ornamentation in the Bivalvia (Mollusca). *Paleobiology*, **7**, 384–393.
- 1988. Adaptive morphology of the shell in bivalves and gastropods. 105–141. In TRUEMAN, E. R. and CLARKE, M. R. (eds). *The Mollusca, Volume 2. Form and function*. Academic Press.
- SIENZEL, H. B. 1971. *Oysters*. N953–N1224. In MOORE, R. C. (ed.). *Treatise on invertebrate paleontology. Part N. Mollusca (3)*. Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas, 1224 pp.
- TAYLOR, J. D. 1976. Habitats, abundance and diets of muricean gastropods at Aldabra Atoll. *Zoological Journal of the Linnean Society*, **59**, 155–193.
- 1977. Diets and habitats of shallow water predatory gastropods around Tolo Channel, Hong Kong. 163–180. In MORTON, B. (ed.). *Proceedings of the 1st international workshop on the malacofauna of Hong Kong and Southern China, 23 March–8th April, 1977*. Hong Kong University Press, Hong Kong, 345 pp.

- 1978. Habitats and diet of predatory gastropods at Addu Atoll, Maldives. *Journal of Experimental Marine Biology and Ecology*, **31**, 83–103.
- 1990. Field observations of prey selection by the muricid gastropods *Thais clavigera* and *Morula musiva* feeding upon the intertidal oyster *Saccostrea cucullata*. 837–855. In MORTON, B. (ed.). *The marine flora and fauna of Hong Kong and Southern China. Proceedings of the 2nd international marine biological workshop, Hong Kong, 1986*. Hong Kong University Press, Hong Kong, 1268 pp.
- MORRIS, N. J. and TAYLOR, C. N. 1980. Food specialization and the evolution of predatory prosobranch gastropods. *Palaontology*, **23**, 375–409.
- CLEEVELY, R. J. and MORRIS, N. J. 1983. Predatory gastropods and their activities in the Blackdown Greensand (Albian) of England. *Palaontology*, **26**, 521–533.
- VANCE, R. R. 1978. A mutualistic interaction between a sessile marine clam and its epibionts. *Ecology*, **59**, 679–685.
- VERMEIJ, G. J. 1977. The Mesozoic Marine Revolution: evidence from snails, predators and grazers. *Paleobiology*, **2**, 245–258.
- 1978. *Biogeography and adaptation. Patterns of marine life*. Harvard University Press, Cambridge, Mass., 332 pp.
- 1987. *Evolution and escalation. An ecological history of life*. Princeton University Press, Princeton, New Jersey, 527 pp.
- WALLER, T. R. 1978. Morphology, morphoclines and a new classification of the Pteriomorpha (Mollusca: Bivalvia). *Philosophical Transactions of the Royal Society of London, Series B*, **284**, 345–365.
- WATTERS, G. T. 1993. Some aspects of the functional morphology of the shell of infaunal bivalves (Mollusca). *Malacologia*, **35**, 315–342.
- WAYNE, T. A. 1987. Responses of a mussel to shell-boring snails: defensive behaviour in *Mytilus edulis*? *The Veliger*, **30**, 138–147.
- WILLIAMS, L. G., RITTSCHOF, D., BROWN, B. and CARRIKER, M. R. 1983. Chemotaxis of oyster drills *Urosalpinx cinerea* to competing prey odors. *Biological Bulletin*, **164**, 536–548.
- WILSON, J. G. 1979. What is the function of the shell ornamentation of *Tellina fabula* Gmelin? *Malacologia*, **18**, 291–296.
- ZAVAREI, A. 1973. Monographie des Spondylidae (lamellibranches) actuels et fossiles. *Centre d'Études et de Recherches de Paleontologie Biostratigraphique (CERPAB)*, **4**, 1–230.

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